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Geology

Published by Field Museum of Natural History

Volume 33, No. 15 November 28, 1975

This volume is dedicated to Dr. Rainer Zangerl

Permo-Carboniferous Fresh Water Burrows

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ABSTRACT

Burrow-casts from fresh-water deposits of the Late Paleozoic have given concrete evidence of the aestivation of the lungfish, *Gnathorhiza,* and the amphibian, *Lysorophus*. The structure of these burrows and inferences concerning the life habits of their occupants are analyzed, with special attention to *Lysorophus*. A previously unknown type of burrow, found in association with those of lung fish is described. It is a large, complex structure, ovoid in cross-section and oriented vertically in the surrounding sediments. By elimination it seems most probable that it was formed by some type of large crustacean, but the precise origin remains uncertain.

INTRODUCTION

Casts of burrows of animals are frequently encountered in the fresh-water deposits of Permo-Carboniferous age. The smaller ones generally result from the activities of various kinds of "worm-like" animals and the larger are generally considered to be burrows of the lungfish *Gnathorhiza*. It is with the larger types of burrows that this paper is concerned. Oddly, it was not until 1954 that any formal note was made of these burrows, although surely they must have been seen before. In that year, Romer and Olson (1954) published a short account of the evidence for aestivation of *Gnathorhiza* based on its burrows from two localities. Since that time many additional Permian sites in the Arroyo, Vale, and Choza

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Formations of the Texas Clear Fork Group and in the Wellington Formation and Hennessey Group of Oklahoma have been discovered. Vaughn (1964) described burrows from the Sangre de Cristo Formation of New Mexico and Carroll (1965) noted burrows in the Pennsylvanian of Michigan. Informal reports carry these sorts of burrows into the Mississippian and tentatively into the Triassic. Carlson (1966) made a thorough study of the burrows at three sites in the Wellington of Oklahoma, giving details of both the burrows and the contained lungfishes.

Ovoid nodules containing coiled specimens of the amphibian *Lysorophus* have long been known from the Arroyo Formation of Texas. In more recent years their range has been extended into the Vale and Choza Formation of Texas (Olson, 1956) and into the Fairmont Shale of the Hennessey Group of Oklahoma (Olson, 1970, 1971). Somewhat cylindrical burrow-casts occur in the Choza and the Fairmont Shale and these too contain skeletons of *Lysorophus*. Although it is quite clear, and has been somewhat casually noted in various publications, that *Lysorophus* was an aestivating amphibian, little attention has been paid to its burrows.

During the field seasons of 1972 and 1973 additional studies were made at several localities which have produced either *Lysorophus* or *Gnathorhiza*. From one site in the Vale Formation of Texas an odd type of burrow which cannot be assigned to either one, or currently to any known Permian animals, has been found. These structures occur in association with "normal" lungfish burrows and will be discussed in the final section of this paper.

LYSOROPHUS

This aquatic-aestivating amphibian is abundant in the formations of the Clear Fork Group, Early Permian, of Texas and equivalent formations in Oklahoma. It was first named from Pennsylvanian deposits in Illinois and has been found at various sites in the Dunkard Series, Early Permian of Ohio, West Virginia, and Pennsylvania. It has been mentioned and described many times in the literature on the Permian. A detailed account of the morphology of the skull was published by Sollas (1920) and recently John Bolt and Richard Wassersug (1975) have published a new study of the skull of *Lysorophus*. A general summary of the habits and probable habitats of *Lysorophus* was given by Olson (1956, 1970) and in 1971 much of the postcranial anatomy was described on the basis of a nearly complete specimen from the Fairmont

	SAMPLE								
	1	2	3	4	5	6	7	8	9
Size groups (centrum lengths in mm.)									
2.0 - 2.9		X						XX	X
3.0 - 3.9					X	XXXX			XX
4.0 - 4.9		XXX			XX	XXXXXXXXX	XX	X	
5.0 - 5.9		XX			XX	XXXXXX	XX	XXX	XXX
6.0 - 6.9	XX	X	XXXX	X		XX	X	X	XX
7.0 - 7.9	X		XX	XXX			XXXX		XXXX
8.0 - 8.9	XX			XX					XX
9.0 - 9.9				X					XXXXXX
10.0 -10.9									X

SAMPLE NO.	n	$\bar{X}$	s	range
1.	5	7.3 ± .35	.79	6.3 - 8.1
2.	7	4.6 ± .47	1.24	2.6 - 6.1
3.	6	6.9 ± .26	.64	6.2 - 7.8
4.	8	7.7 ± .51	1.44	5.5 - 9.9
5.	7	5.5 ± .58	1.52	3.5 - 7.8
6.	20	5.0 ± .32	1.42	3.4 - 6.7
7.	12	6.73 ± .57	2.00	4.5 - 8.5
8.	7	4.49 ± .63	1.66	2.0 - 6.7
9.	21	7.10 ± .63	2.86	2.6 -10.0

FIG. 1. Some examples of the size distributions in samples of *Lysorophus*. The pooled means cited in the text and used in the plot in Figure 2 were determined from a much larger suite of samples of the same general character. Samples 1 through 6 are from the Arroyo; samples 7 and 8 are from the Vale; sample 9 is from the Choza. In 1 through 8 the specimens were preserved, tightly coiled, in dolomitic nodules. Specimens in sample 9 were not from nodules and not tightly coiled. The first eight were from the aestivation stage and the last from the free-swimming phase. n, number of individuals in sample; s, sample standard deviation; $\bar{X}$ sample mean.

Shale of the Hennessey Group of Oklahoma (Olson, 1971). This, then, is a well-known amphibian.

In spite of this the taxonomy remains unsettled. The genus and species, *Lysorophus tricarinatus*, were named on the basis of fragmentary vertebrae from an Upper Pennsylvanian site near Oakwood, Illinois (see Olson, 1946). The name was carried over to the Texas specimens and also to those from the Dunkard. It is not at all certain that the Texas specimens belong to the named species and there is considerable question even about the validity of the name *Lysorophus*. The taxonomy, although badly in need of a thorough review, is not germane to the purposes of this paper, and we will use the name *Lysorophus* to refer to the Texas and Oklahoma materials, without a species name, but with the conviction that all of our materials do pertain to but a single species.

The remains of *Lysorophus* reflect two aspects of its living habits — a free-swimming phase and as aestivating phase. The great majority of specimens have come from the latter and it is with these that we will be principally concerned.

Three aspects of the aestivating phase are of particular interest. First, as has been noted briefly in earlier papers, the fossils characteristically occur in local concentrations, each occupying at most an area of a few square meters. Second, each such concentration tends to yield specimens of about the same size (fig. 1). Based upon measurements along the base of the centra of the dorso-lumbar vertebrae (in which variation along the column as measured by the coefficient of variation "V" in individuals ranges from about 1.5 - 3.0) pooled means from various samples of 2.5, 4.5, 7.2, and 10.0 mm. have been obtained. Even smaller animals are known with centra no longer than 1 mm., but not in sufficient quantity or well enough preserved for reliable estimations of means. As shown in Figure 1, for some representative samples, there is considerable variation around the mean at each of the sites, but for the most part different sample groups, subjected to a standard t-test of means, prove to be significantly different at the P = .05 level.

In these samples the animals are tightly coiled and the nodules which they form are ovoid (pl. IE). Most have only one individual but some have two or three. There is no distinct, regular boundary between the nodules and the surrounding sediment, but there is a

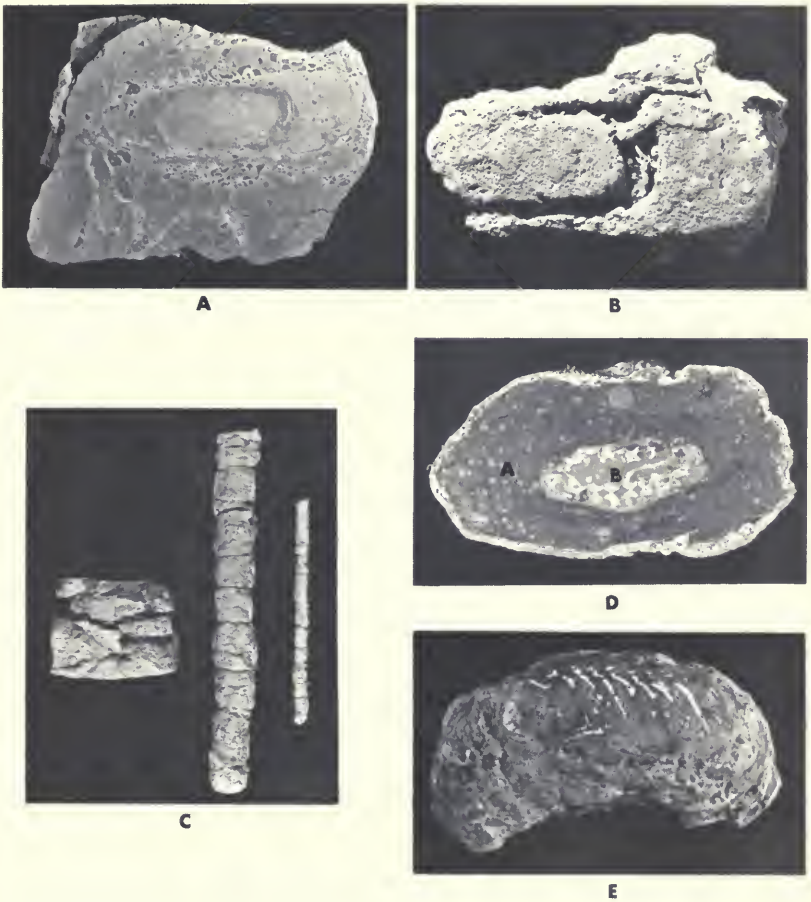

PLATE I. **A**, A cross-section of a burrow-cast of undetermined origin from the Vale Site 1919. × about ½. **B**, An acid etched cross-section of a burrow-casts from the same site at A; × about 1. **C**, Segments of burrow-casts from the Vale site 1919: segments on right are from lungfish burrows; on left is from the undetermined casts also shown in A and B. × about ¼. **D**, Cross-section of a *Lysorophus* burrow-cast with part of the animal shown in place. From a burrow of the type shown in Plate IIB. × about ⅓. (For explanation of letters see Figure 3.) **E**, A partial nodule of *Lysorophus* from the Arroyo Formation showing curved outline of nodule controlled by coiling of individual specimen: × about ¾.

marked difference in composition, with nodules being very high in dolomite, with a small admixture of quartz and feldspar and the surrounding sediments being predominantly quartz. The nodules weather cleanly from the sediments, being much more resistant to chemical actions of the ground water and mechanical weathering.

From the Choza Formation of Texas and the Fairmont Shale of the Hennessey Group in Oklahoma, has come a series of samples with larger individuals of *Lysorophus* in which the mean, pooled, vertebral length is 11.8 mm. Some of the individuals have lengths as great as 13.5 mm. approaching the large Dunkard lysorophid *Molgophis* in size. In these same formations there are also smaller individuals, but these do not exhibit the clumping pattern found in the Arroyo and Vale, are not coiled, and are not encased in dolomitic nodules. They appear to have been preserved from the free-swimming stage of life.

The third point of special interest is that the large individuals from the Choza and Fairmont occur in a different sort of a burrow, being found in elongated burrow casts with elliptical cross-sections (pl. ID; IIB). The specimens from these kinds of burrows, like those in the nodular burrows from different sites, fall into a limited size range, but in this case only one size group, with a mean of 11.8 and a range from about 10.5 - 13.5 mm. has been found. The relative amounts of quartz, feldspar, and dolomite in the matric and in the burrow-cast are shown in Figure 3. A regression of the mean sizes on ontogenetic time, in which it is assumed that the different size groups represent periodic, perhaps annual aestivation stages, shows a rather typical growth curve (fig. 2). The final stage indicates a continuation of a slight reduction in the relative growth rate established between the two succeeding stages. The most logical interpretation is that the large forms represent an additional growth stage, not recorded in earlier formations and that they also assumed a somewhat different mode of burrowing.

Three features then characterize the aestivation habits of *Lysorophus*: (1) clumping of individuals; (2) size segregation in the clumps; and (3) different habits of burrowing in the largest size group as compared to those of the small animals. Various studies of living amphibians and fishes, and even invertebrates, suggest reasons why these characteristics may exist. If we assume, as we have, that the basic motivation for burrowing was aestivation, then the difference in behavior between size groups may relate to differences in:

1. Physiology;
2. The substrate;
3. Water depth;
4. Climate at different times;
5. Function and morphology.

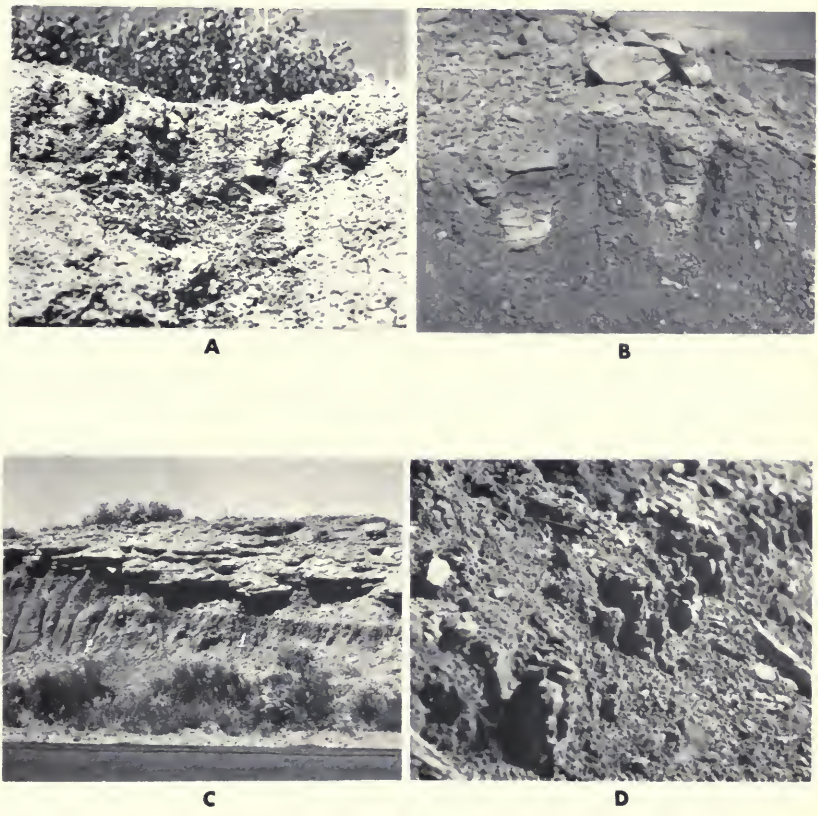

PLATE II. **A**, Lungfish burrow-casts in place at site #3 of Carlson (1968) (Perry 5, Olson, 1970). **B**, Two burrow-casts of *Lysorophus* in place at site in the Choza Formation of Foard County, Texas. **C**, The Vale outcrop of burrow-casts at Vale site 1919. **D**, Closeup of burrow-casts at site shown in C.

These are not exclusive and are somewhat difficult to differentiate even among living animals, becoming evident only after careful experimental work and field observations. The problems with fossils are, of course, much more acute.

It has been shown in salamanders that water loss is substantially less in large than in small animals under similar circumstances (Ray, 1958, Spight, 1968), and that aggregation and coiling reduce both the rate of water loss and oxygen consumption. This has been demonstrated for the tiger salamander, *Ambystoma*, as well by Gehlbach et al. (1969). *Siren* and plethodontids occur in burrows in both coiled and straight positions, but when occupying

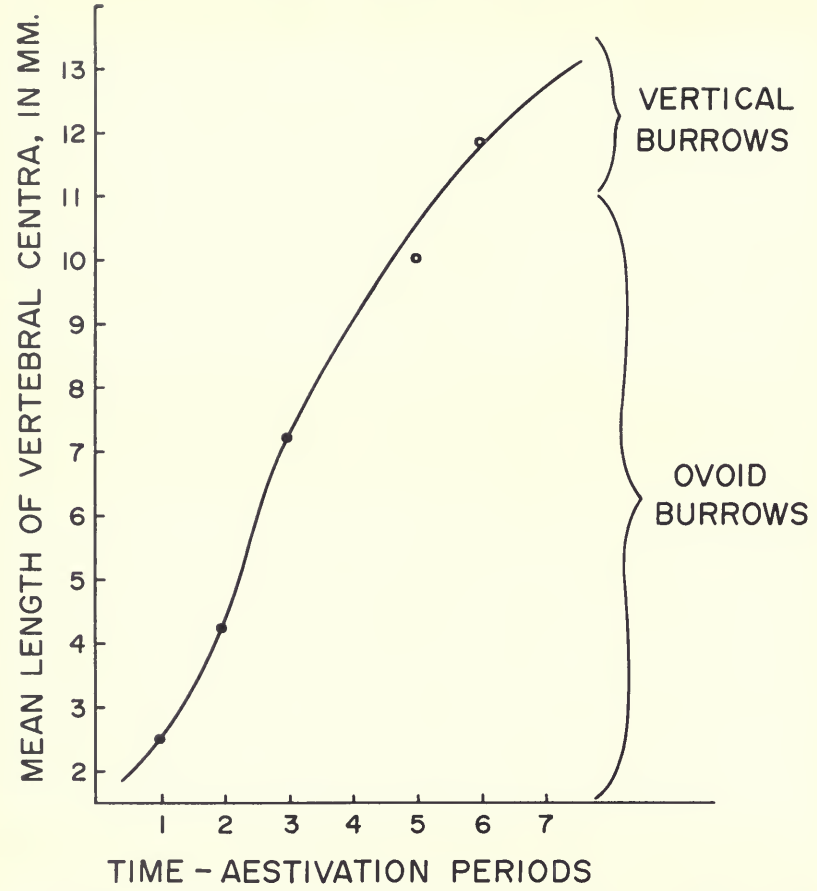

FIG. 2. A regression of the mean length of vertebral centra, pooled for several samples at each point, on aestivation periods. It is assumed that aestivation periods mark equal time units, perhaps annual.

burrows which they have made themselves they are usually coiled. Where there is periodic aridity, plethodontids assume a coiled position (Heatwole, 1960). On the other hand, Ray (1958) has shown that animals obtained from moist areas do not coil under experimental conditions even when drying is artificially induced. Coiling habits differ between species relative to body structure. *Ambystoma*, for example, is only able to form a tight S-curve, whereas plethodontids are able to form full coils. A change in form and size in ontogeny might bring about similar behavioral differences between growth stages within a species and perhaps this may have resulted in the differences in burrowing behavior between the small and large specimens of *Lysorophus*.

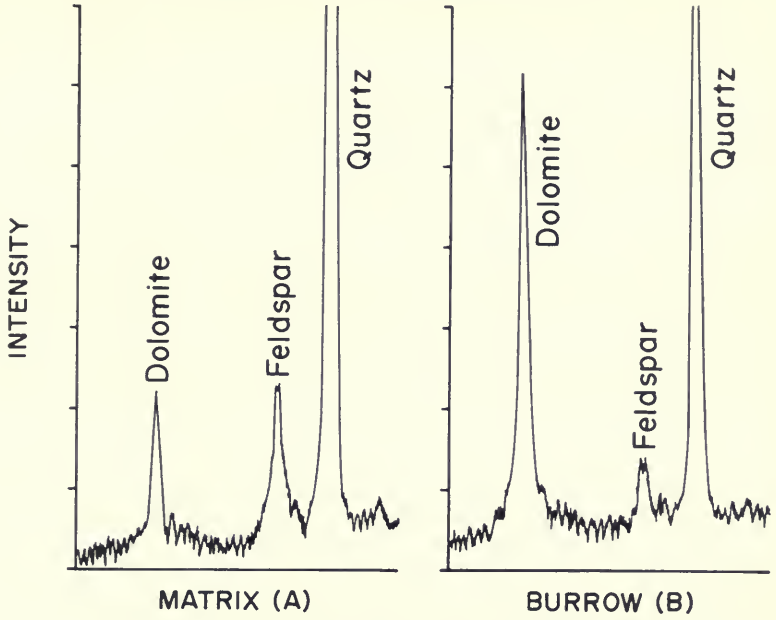

FIG. 3. The results of X-ray analyses of the matrix and burrow-cast of a large *Lysorophus* from the Choza. The burrow-case is of the type shown in Plate IIB. Relative proportions of quartz, feldspar, and dolomite are shown. Note the relatively high proportion of dolomite in the burrow cast as compared with the matrix. Letters A and B refer to the positions of the samples as shown in Plate ID.

The hardness of the substrate and its capacity to hold water also are important to the nature of the burrowing amphibians. Many burrowers penetrate, where possible, to the moist zone of the substrate. Shallow burrows are formed where the substrate tends to remain moist close to the surface. Substrates that lose water rapidly are less suitable for burrowers than those which retain water and thus both compositon and the texture of the substrate are important. Heatwole (1960), on the basis of experiments with different substrates, concluded that "probably coiling in burrows indicates an inability to penetrate the substrate farther to reach favorable conditions." He noted also that animals tended to move about in search for suitable sites for burrowing. If the most favorable sites differed somewhat for different size groups, then a segregating site selection might take place.

Depth of water in which different size groups live and in which they burrow for aestivation may also be a consideration. *Protopterus*, for example, tends to be distributed with the larger animals in deeper water and smaller animals in shallower water. As conditions

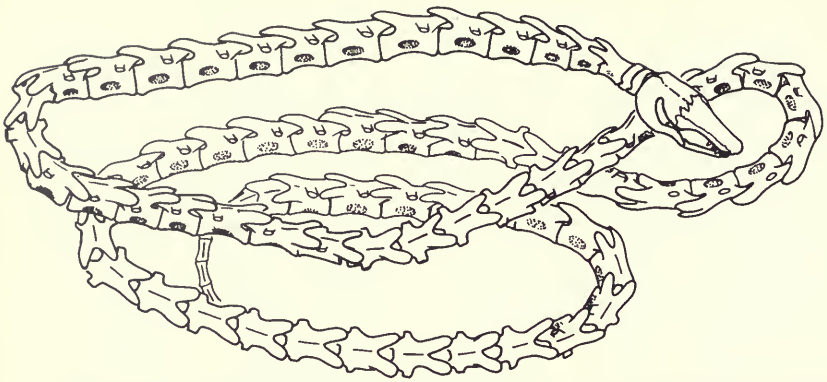

FIG. 4. The pattern of coiling of *Lysorophus* in large, vertical burrows of the type shown in Plate IIB. The reconstruction is based on analysis of several burrows both from the Choza Formation of Texas and the Fairmont Shale of Oklahoma.

leading to aestivation set in, burrowing tends to occur in the main areas of habitation, resulting in some size segregation.

Climate is a controlling factor in aestivation, determining not only where the phenomenon will occur but also strongly influencing the form it will take. In the case of aestivation of extinct animals over a period of geological time, the factor of climatic change may be very important. Clearly the climate changed somewhat from the Arroyo to the Choza times in Texas and similar changes seem to have occurred in Oklahoma. There was a tendency for increased aridity, but also, it appears, there tended to be an increase in the number of relatively small, but permanent lakes near the coast lines. It is in such deposits, formed in small lakes, that *Lysorophus* is found in the Choza and in the Fairmont Shale of Oklahoma. The smaller animals, with central lengths of less than 10 mm. do not appear to have aestivated under these circumstances. Samples contain a wide range of size groups and specimens are not found tightly coiled in nodules (see fig. 1, column 9). A few such sites have been found in the Vale, but they are rare. The larger animals, however, did aestivate, occurring in elongated, elliptical burrows, in loose, open, spiral coils (fig. 4, pl. ID, IIB).

It may be that the differences in coiling patterns between these large forms and those of the tightly coiled smaller ones from the Arroyo and Vale Formations arose merely because the large individuals mechanically could not coil tightly. Being less subject to dessication because of their size, these large individuals probably could tolerate the conditions of a single burrow even though they

were loosely coiled. This does not explain the fact that the smaller ones did not aestivate at all. It also does not explain why the very large individuals have been found only in the Choza and Hennessey and not in any of the many samples from earlier formations. Perhaps only during the Choza and Hennessey times were the climatic conditions favorable for continued growth, or perhaps the substrates of earlier sites were not suitable for larger forms which could not coil tightly and aggregate.

Any solution is necessarily speculative. What seems to be the most likely explanation, however, relates to the special conditions of the small permanent lakes. *Lysorophus* does not appear to have lived in large, open bodies of water. The permanent small lakes may have provided optimal conditions for growth, but if, as seems likely, they were subject to periodic partial, but not complete, drying, then it could have been that only the largest animals would have found it necessary to aestivate, whereas the smaller could continue their free existence in shallow waters under somewhat restricted, but favorable conditions.

The large animals probably were unable to cope with limited, shallow water and reduced food supplies, but could survive in burrows in which they were loosely coiled. This interpretation fits the evidence from both sites at which the large burrows occur. The distribution by size of a sample of the free-swimming forms from the Choza site is shown in the last column in the histograms in Figure 1. There is no clustering of size groups and, as noted earlier, the specimens do not occur coiled in dolomitized nodules.

This is at least a logical explanation for the differences in burrow types and the occurrence of large animals only in the Choza and Fairmont Shale of the Hennessey. It does not explain why groups of similar sizes occur in isolation in earlier formations. Perhaps there was some sort of schooling behavior, such as various fishes show, or some control by depth of water. The non-segregated distribution of individuals from the free-swimming samples suggests, however, that this was not the case. Rather, it appears more likely that the grouping was based on modest substrate differences which had advantages for one or another size group with respect to easy penetration and moisture retention. Site selection may have been the most important factor in producing the size groupings. This is subject to testing in the field, but currently at least, access to the critical sites is not permitted by the land owners.

GNATHORHIZA

The descriptions of the burrows of *Gnathorhiza* in Romer and Olson (1954) and the detailed study by Carlson (1968) make it necessary to touch only on some points which serve to differentiate lungfish burrows from other types. Some burrows in outcrop, where the sediment has been partly cleared away, are shown in Plate IIA. The general shape is fairly distinctive, but the primary criterion for recognition of lungfish burrows, of course, is the presence of well-preserved remains of fishes in aestivating position. In the site shown, site #3 of Carlson, fish are abundant, but in some other sites the burrows are largely barren.

From the occupied burrows it is possible to obtain information upon the general morphology of the burrow-cast and to carry this over for interpretation of barren burrows elsewhere. In these latter cases, of course, there must remain some doubt, for other burrowing animals can make structures which are quite similar. Several localities of the Early Permian in Oklahoma and Texas have well-preserved remains of lungfishes. The best are at Romer's Reed Ranch locality in Wilbarger County, Texas and at Carlson's site #3 in Oklahoma, near the town of Perry. This is Perry site 5 as designated by Olson in 1967. Also lungfish are abundant but badly macerated at Carlson's site #1, which is Perry site 1 in Olson, 1967.

Beyond the presence of preserved fishes, some morphological features of the burrow-casts are more or less diagnostic. When well preserved and not severely weathered, the cast consists of an outer shell and an inner core, with a more or less circular cross-section. As described by Carlson (1968) at his site #1, the outer shell contains packed scales and small bones, indicating some compacting action by the fish during construction of the burrow. This outer shell is usually lost during weathering leaving only the inner core, in which the fish is preserved, if present at all. This core consists of a long cast of the inner chamber and ranges from about 1.5 - 10 cm. in diameter, in different casts, and may be as much as 50 cm. in length. The diameter of individual burrows changes very little from top to bottom, but some tend to narrow slightly in the lower portions. The casts are always nearly vertical in the enclosing sediments, not departing more than some 5 - 8 degrees from verticality. Plates IC and II A, C, D, show some of the "burrows" in place and others removed from the matrix.

When the outer shell is present, the outer surface may be quite irregular, although still roughly circular in cross-section. The inner

chamber has a very regular outer surface and under some circumstances shows strong slickensides oriented nearly vertically. The chemical composition of the core differs somewhat, depending upon whether or not large amounts of organic material were present. Those which have well-preserved fish remains are highly dolomitic as compared with the surrounding matrix. Carlson (1968) pointed out this dolomitic character and it has been confirmed at several other sites as well (fig. 5). Casts from two sites in the Vale, however, in which fish remains are absent, or nearly so, have a much lower increment of dolomite, being composed mostly of quartz with only small amounts of dolomite and feldspar.

Burrow-casts that are well preserved and show most of the structures noted above can be referred to the lungfish *Gnathorhiza* with considerable confidence. Problems arise when there are deviations from this pattern, and this is what happened in the case of a new burrow site in the Vale, as discussed in the following section.

BURROWS OF THE VALE SITE 1919

This locality lies on Texas Farm Road 1919 near the boundary between Baylor and Foard Counties. It is quite near one of the sites from which lungfish burrows were first described by Romer and Olson in 1954. The outcrop along the roadcut is shown in Plate IIC, D. Typical burrow-casts of *Gnathorhiza* are present. These range in cross-section dimension from 1.5 - 6.0 cm., all are long and have a cup-shaped base. These structures, of course, were immediately identified as lungfish burrows and some of them carry scattered remains of *Gnathorhiza* bones and scales. Along with them are some rather large, vertical structures with more elliptical cross-sections, these are enclosed in an irregular shell which contains darker, irregular fragments of rock which give the appearance of being brecciated. These also were at first thought to be lungfish burrows which had retained an outer shell, as had those at site #1 of Carlson. After cross-sections had been made (fig. 6; pl. IA), problems in reconciling the two types of burrows were encountered as discussed below.

The matrix surrounding the burrows of this exposure contains remains of *Lysorophus,* of a small nectridean close to *Peronedon* of the Fairmont Shale of Oklahoma (Olson, 1970), and of a small, undetermined reptile with a skull length of about 1 cm. Fragments of *Gnathorhiza* are occasionally encountered. As is usual in

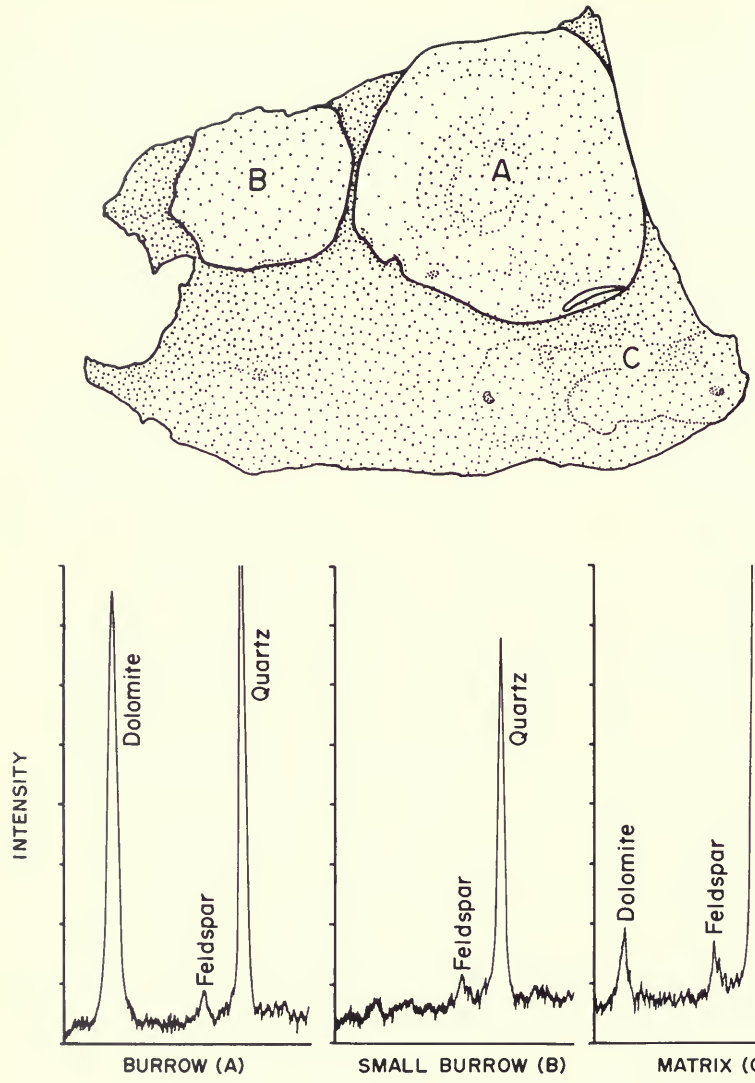

FIG. 5. Above: Diagram of a cross-section through the base of a burrow, A and a "reduction halo" of a second burrow, just below the burrow in shale, B. C represents a sample from the matrix. Below: An X-ray analyses showing the relative proportions of quartz, feldspar, and dolomite at A, B, and C. Note the relatively high proportion of dolomite in the burrow-cast, in which a lungfish was preserved, but its absence at B and small relative amount at C.

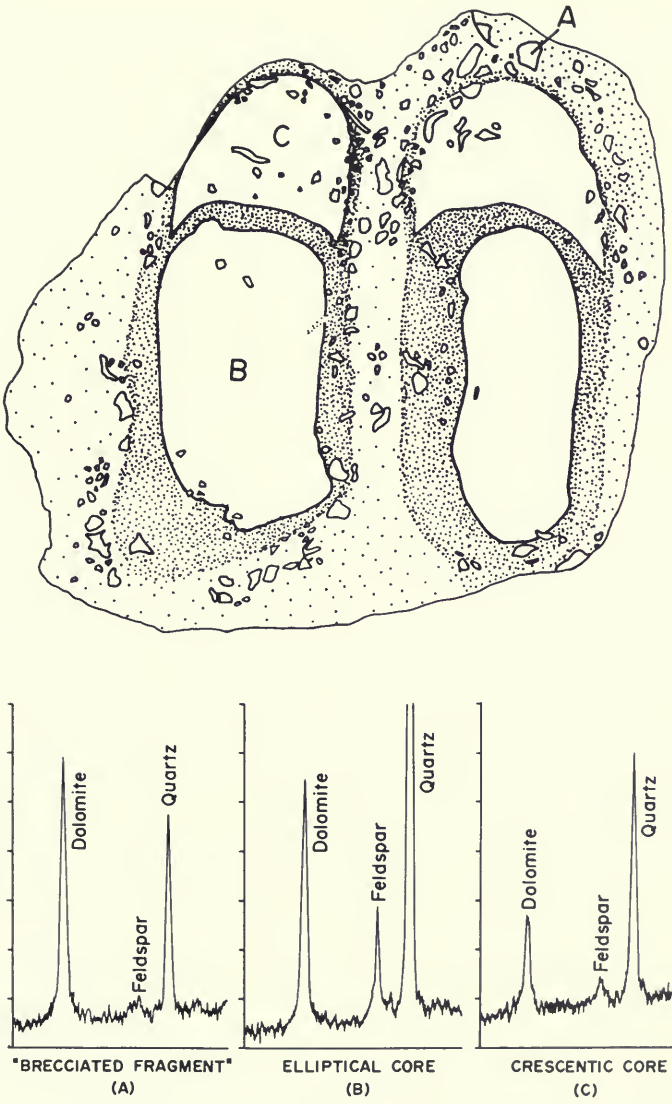

FIG. 6. Above: Diagram of the cross-section of two adjacent burrow-casts with elliptical cross-sections of the type shown in Plate IA, B, and C (left figure). Below: results of X-ray analyses showing relative proportions of quartz, feldspar, and dolomite at sample sites A, B, and C (above). **A** is one of the deep brown "brecciated" fragments around the burrow cast (see also pl. IA). **B** is the elliptical core and **C** the crescentic core. Note the relatively high proportion of dolomite in the "brecciated" fragment contrasting with the relatively low proportion at B.

Permian red-beds remains of invertebrates are almost non-existent. A few fragments and impressions of very small pelecypods have been found, but that is all.

It appeared that this outcrop offered a chance for a detailed study of the internal structure of lungfish burrows and additional analyses of conditions of deposition. Several blocks of burrows were taken from the unweathered parts of the deposit and these were "dissected" and serial cross-sections of the burrows were cut. The composition of the burrows and matrix were subjected to X-ray analyses by Dr. Keith Chave. A number of unexpected factors were discovered.

The burrow-casts with circular outlines, lungfish burrows, could not be identified more than a few inches back of the outcrop surface. Etching with strong acid, X-ray analyses, and studies of cross-sections under light microscopes revealed no trace of them. On the other hand, the more elliptical structures with "brecciated" outer shells continued to be present in abundance. First we thought that the cores of these elliptical structures produced the circular casts of the lungfish burrows. The composition of both is very similar, being predominantly quartz, with small amounts of dolomite and feldspar (fig. 5). The shape of the cores of the elliptical structures, however, shows that this cannot be so. There seems to be no way by which these cores could have modified consistently from their characteristic shapes to form casts with nearly circular cross-sections.

The structure of the cross-sections of the elliptical burrows is shown in Figure 6 and Plate IA. The outer shell, with dark fragments, which give a brecciated appearance, is consistently present. This encloses the inner parts of the structure for its full length of about 50 cm. The enclosed area, in cross-section, consists of two distinct core structures. One is an elliptical core which is surrounded by a deeper brown zone. The material of this zone is more soluble in strong acid than in the core and etches as shown in Plate IB. The second core structure is crescentic and the arms of the cresent pass into the outer shell, as shown on the etched specimen. The deeper brown, more soluble zone, separates it from the elliptical core. The relative composition of the different components is shown in Figure 6.

The deep brown fragments in the "brecciated" part of the structure are high in dolomite relative to quartz and compared to

the core and the surrounding matrix. This suggests that a high content of organic material was present during their formation, analogous to the situation of lungfish burrows in which fish remains are well preserved.

The structure of these casts is quite clear. What produced them is at present uncertain. Unlike many *Gnathorhiza* and *Lysorophus* burrows, they carry almost no recognizable organic remains, either of complete animals or washed-in fragments. Clearly, they are not burrows of *Lysorophus* and no other aestivating amphibians are known from this time in the Permian. If they are vertebrate burrows, it would appear that they must be lungfish or some otherwise unknown animal. In any case, it appears likely that some remains of the producer would have been found within the sediments, and none has.

The outer shell would appear to be the result of some sort of action by the occupant. *Gnathorhiza* seems to have packed its walls, as described by Carlson (1968). In *Protopterus*, as shown by Johnels and Svensson (1955), drying of the sediment and of the occupant of a burrow results in contraction of both, and a water resistant cocoon is formed by the lungfish. Such alterations might leave a fossil record in the form of modifications of the outer margins of the burrow. Some specimens of *Protopterus* do have sediment between the parts of the body folded in the burrow and conceivably the brown layer between the two chambers might be some such feature, although very different from that of *Protopterus*. The burrows from the Vale, however, are totally different in shape from those of *Protopterus* and any analogies seem far-fetched. Added to this is the fact that the aestivation burrows of *Gnathorhiza*, the only known lungfish from this time, while similar in being elongate and vertical, are very different in internal structure.

It appears then that the burrows may either be those of some invertebrate or else are inorganic in origin. They clearly are not tree roots and any inorganic origin poses many more problems than an organic one. The absence of remains of a possible invertebrate producer poses no serious problem in view of the fact that their remains are very rarely preserved in the red sandstones and clay-shales of the Early Permian of Texas and Oklahoma. Small conchostracans, small pelecypods, and, of course, insects are known from beds of the Lower Permian, but these occur mostly in the dolomites and only pelecypods are found in the red shales. These

are always small and usually preserved as impressions. None of these known invertebrates can be considered as candidates for the formation of the elliptical burrows, on a size basis alone. The fact that these are fresh-water deposits generally limits the kinds of invertebrate organisms which could have been present to make the burrows to fresh-water molluscs, pelecypods or gastropods, and to crustaceans. The fresh-water molluscs do not seem to be good candidates, in view of the complex nature of the burrows, so that it seems that these may be the work of some large crustaceans, by elimination, however, rather than because of any reasonable analogue among known moderns.

Fossil burrows of a marine decapod, termed *Ophiomorpha* and made by animals close to *Callianassa*, were described in detail by Hester and Pryor (1972). Shapes are vaguely similar in cross-section and the burrows are elongated, but they are irregular and curved and twisted. The most pertinent point in their discussion with reference to the present case is that the burrows which they described were in some instances lined with fecal pellets. The red-brown "brecciated" fragments in the Permian burrow walls have somewhat the appearance of broken coprolites from beds of this type and their dolomitic nature suggests a possible organic content during their formation. They could, conceivably, represent a wall-lining by fecal material.

The two different structures of the core indicate a complex occupancy of the burrows, for which no very plausible explanation has been forthcoming. Was there a "living chamber," the elliptical core, and a second chamber, say for water circulation or waste disposal? Was this an elongated animal that somehow folded over to occupy the two parts of the chamber with, for example, some sort of siphon to the surface in one or the other? Or are the two chambers the result of some sort of differential shrinking with drying and contraction of the sediments which somehow produced the more soluble external coating of the elliptical cross-section? Was this burrow some sort of a "brood chamber" either for an invertebrate or a vertebrate? Is it possible, for example, that *Gnathorhiza*, like some modern lungfish, did have brood-burrows different from aestivation burrows and that is what we have found?

We don't know and currently have no favored explanation. It is possible that more precise analysis of the composition of the various parts of the structures will give additional information, and this is being investigated. Most likely, however, it will be necessary to find

a reasonable modern analogue, which now is either not known or at least not known to us, or to find circumstances in which the animal has been preserved in the burrows.

ACKNOWLEDGMENTS

The research leading to this paper was supported by a National Science Foundation Grant GB 31283X. Field work was done with the aid of Mr. Gary Johnson of Southern Methodist University and Mrs. Lila Olson. Laboratory preparations of the materials for study were carried out by Mr. Richard Lassen, Museum Scientist at the University of California at Los Angeles. The X-ray analyses were carried out by Dr. Keith Chave of the University of Hawaii. We are sincerely grateful to each of these persons and to the National Science Foundation for their indispensible aid.

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